

BEHAVIOR OF THE SEA PANSY *RENILLA KOLLIKERI* PFEFFER
(COELENTERATA: PENNATULACEA) AND ITS INFLUENCE
ON THE DISTRIBUTION AND BIOLOGICAL
INTERACTIONS OF THE SPECIES¹

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This paper describes various behavioral patterns of the sea pansy, *Renilla kollikeri* Pfeffer (Alcyonaria: Pennatulacea), and their influences upon the species' distribution and biological interactions. The study of cnidarian behavior has long focused on patterns associated with either locomotion or feeding (reviewed in Mackie, 1974). However, during the last twenty years the predator-escape behavior of certain actinians has been examined (reviewed in Ross, 1974), and more recently, intraspecific and interspecific "aggression" among species of Actinaria has also been described (Francis, 1973; Lang, 1971, 1973). Few studies, however, have surveyed the behavioral repertoire of a single species and analyzed its role in determining the species' distribution and predator-prey interactions.

Previous work on pennatulacean behavior is limited. Recent papers describe burrowing in the genera *Pteroides* and *Veretillum* (Titschack, 1968; Buisson, 1971, 1974), the diurnal activity patterns of *Cavernularia obesa* (Mori, 1960) and *Scytaliopsis djiboutiensis* (Magnus, 1966), and the predator interactions of *Ptilosarcus guernei* (Birkeland, 1974). The only reports which discuss the behavior of the sea pansy are physiological in nature. These reports discuss muscular movement and colonial coordination (Parker, 1919, 1920b; Anderson and Case, 1975), water movement (Parker, 1920a), respiration (Chapman, 1972) and bioluminescence (Bertsch, 1968; Buck, 1973; Anderson and Case, 1975).

Renilla kollikeri is an abundant member of the shallow, sand bottom fauna of the southern California coast. It inhabits regions of strong turbulence. In sandy, nearshore subtidal areas (to depths of 10 meters), the drag of the ocean swell generates strong, multidirectional bottom currents (velocities of more than four meters per second have been recorded at a depth of three meters). This back-and-forth wave surge, which strengthens as depth decreases, is strong enough to suspend and move a layer of sand to and fro along the bottom. This movement not only buffers the fauna but buries animals under shifting sands. *Renilla* displays many morphological and behavioral features adaptive for life in this turbulent habitat.

The behavioral patterns described and experimentally analyzed below are concerned with three broad aspects of the biology of the sea pansy. First, the maintenance of position on the bottom, particularly the responses to increased water

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movement, burial by shifting sediment, and displacement from the substrate are discussed. Secondly, the species-specific escape behavior from the nudibranch, *Armina californica*, and other predator interactions are described; and thirdly, the food and mode of feeding of the colony are considered. These behavioral patterns are particularly adaptive to and influential in the local distribution of the species.

MATERIALS AND METHODS

Field observations and experiments were conducted using SCUBA equipment in water depths of 3 to 15 meters. The primary study site was at Zuma Beach, Los Angeles County, California, a 6 kilometer long, southwest-facing sand beach, 35 kilometers northwest of Los Angeles, California. The beach is exposed to the open ocean and the surf ranges from 0.3 to 4.0 meters in height throughout the year. Comparative observations were made at Santa Barbara Harbor, Santa Barbara County and at Scripps Beach, San Diego County, California. Laboratory observations and experiments were conducted at the University of California, Los Angeles, and the Santa Catalina Marine Biological Laboratory. The experimental animals were collected by hand and maintained at ambient sea temperatures in both closed (UCLA) and open (SCMBL) circulating seawater systems.

The effects of water flow on *Renilla* were studied in both field and laboratory. In the laboratory animals were allowed to anchor in a layer of coarse sand in various sized aquaria. A water current was directed across the upper surface of the colony from a plastic tube 1.3 cm in diameter. Velocities were measured with

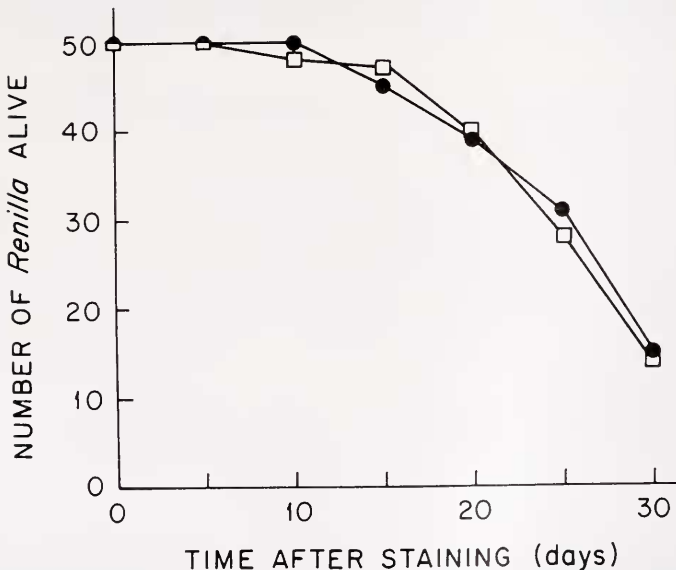


FIGURE 1. Laboratory survival of dyed (boxes) and undyed (closed circles) *R. kollikeri*. The animals were maintained at 13° C. No significant difference in survivorship was observed ($P > 0.5$; chi-square test).

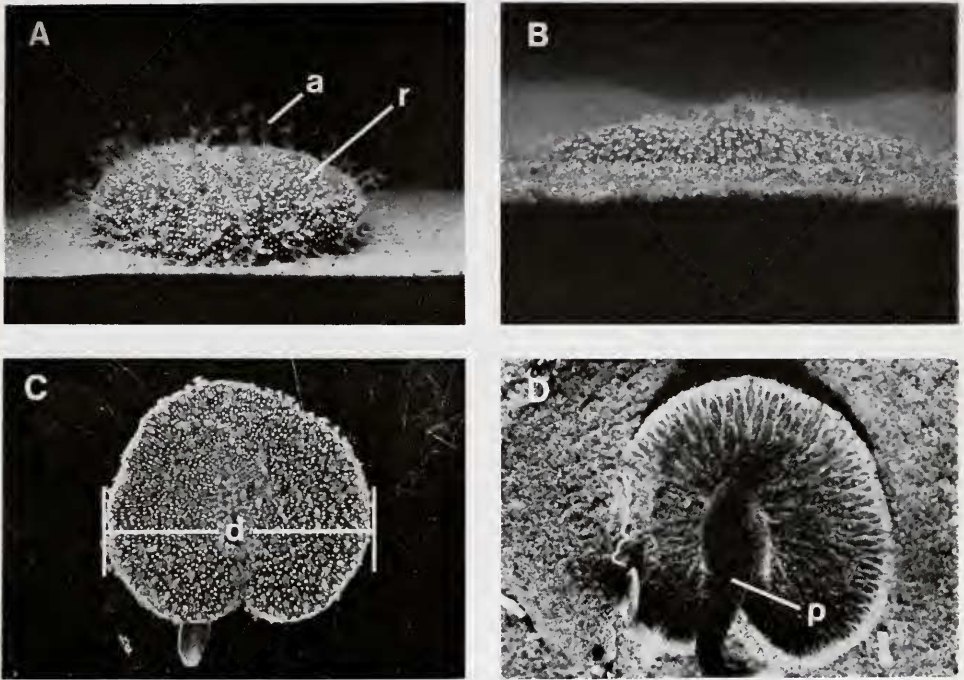


FIGURE 2. *Renilla kollikeri*: A. An expanded colony in still water. Note expanded autozooids (a). B. Deflated rachis characteristic of colony when in moving water and while reanchoring. C. Dorsal surface of rachis showing measure of diameter (d). D. Ventral surface showing peduncle (p). The diameter of the *Renilla* depicted is 65 mm.

a calibrated bead flowmeter (Kontes Flow-Watchman). Field water velocities were determined with a hand-held flow meter (Kahl Scientific Instruments Corporation: Model 005WA120).

Individuals were marked for field study by staining with the vital dye Nile Blue Sulfate. Animals were placed in a 5.0 per cent solution of dye in sea water for no more than three to five minutes. In high concentration or after prolonged exposure, the dye is caustic to the animals. However, stained *Renilla* exhibited the same survival over a two month period in the laboratory as unstained animals (Fig. 1). Furthermore, stained animals were in excellent condition five months after release in the field.

Field movement experiments lasted from six hours to two months. Displacement of dyed animals was measured with a polypropylene line marked in meters from a reference stake driven into the sand at the center of the released group.

All feeding experiments were conducted in the laboratory. Suspensions of potential prey items ranging in size and form from unicellular algae (30 to 50 microns in length) to *Artemia* nauplii and copepods (0.1 to 0.4 mm in length) were pipetted into a chamber containing a sea pansy. Subsequent interactions

between predator and prey were observed at low light levels through a dissecting microscope.

The following anatomical terms will be used throughout the paper. The principal body regions of *Renilla* are the rachis and the peduncle. When a colony is anchored on the bottom, the rachis lies flush against the substrate (Fig. 2a, b). Two different types of zooids are interspersed on its dorsal surface: polypoid autozooids, which function in feeding and reproduction, and siphonozooids, which function in irrigating the colony. Rachis height, or thickness, is the maximum distance between the dorsal and ventral surfaces. Rachis diameter (or size) is the distance across the rachis at right angles to the median line (Fig. 2c). The peduncle is a column of tissue which projects from the ventral surface of the rachis and anchors the colony when it is inserted into the sand. When anchored, the tip of the peduncle is generally bulbous.

OBSERVATIONS AND RESULTS

Maintenance of position

The rachis. The rachis alters its degree of inflation (here defined as height/diameter) in an inverse relation to the velocity of water flowing over it (Fig. 3).

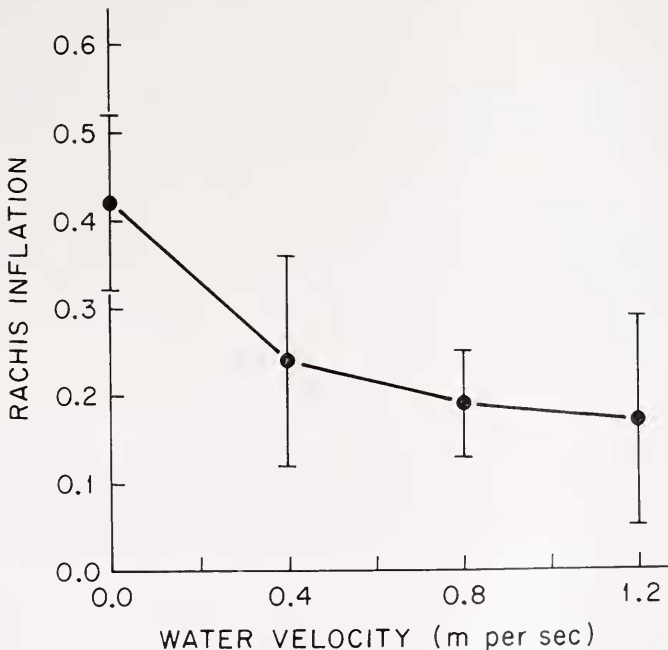


FIGURE 3. Inflation of rachis with respect to velocity of water flow. Inflation is ratio of rachis height to rachis diameter. Samples consisted of 40 animals which ranged from 20 to 90 mm in diameter and were exposed to flow for 30 minutes. There was a significant difference in the means of the samples ($P < 0.01$; ANOVA). Vertical bars represent 95 per cent confidence intervals.

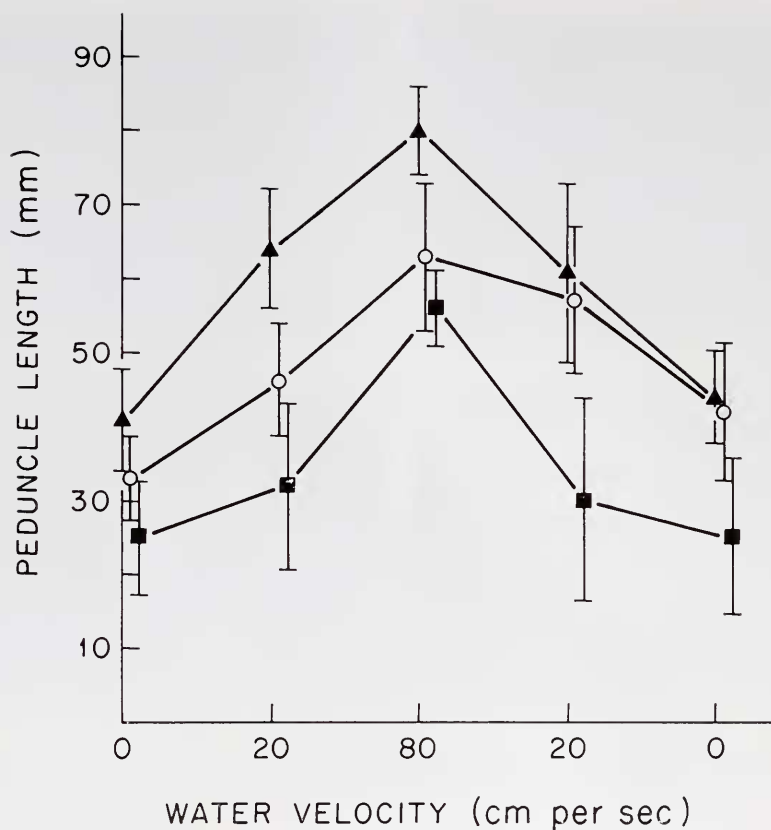


FIGURE 4. Peduncle insertion with respect to water flow velocity. Peduncle length measured after five hours at each of the five experimental water velocities. Three size classes are represented: triangles represent colonies 61 to 80 mm in diameter ($n=17$); circles = colonies 41 to 60 mm in diameter ($n=21$); and squares = colonies 21 to 40 mm in diameter ($n=13$). Mean peduncle lengths differ significantly at each experimental water velocity ($P < 0.001$; Kruskal-Wallis test). Mean of control group (33.4 mm; s.d.=8.1) kept in still water did not differ significantly from that of the experimental group in still water ($P > 0.5$; Student's t -test). Vertical bars represent standard errors.

As a water current (directed across the dorsal surfaces of groups of 20 various-sized animals) increased in velocity from 0 to 1.2 meters per second the height-to-diameter ratio of the rachis fell. In most cases rachis diameter did not change. The response occurred within a few seconds of the increase in water velocity. A group of similar-sized control animals maintained in still water showed no change. Although the response was reversible, animals returned to slower water did not respond as quickly. A similar response was seen in the field. On days of little surge, rachis inflation was noticeably greater than on days of moderate surge.

The peduncle. *Renilla* anchors itself in the substrate with its flexible and extensible peduncle. Peduncle extension varied in a direct relation to the velocity of water flow across the rachis. Figure 4 illustrates a laboratory experiment in which

animals were subjected to different current velocities. A group of various-sized sea pansies was placed initially in still water for five hours. Half of the animals were then uprooted and their rachis diameters and peduncle lengths were measured. The uprooted group was then subjected to five hour periods of various currents (0, 20, 80 and 20 cm per second). After each five hour period the rachis diameters were measured *in situ* and the peduncle lengths measured immediately upon uprooting. The other 25 of the original set of animals served as a control, maintained in still water and measured at corresponding five hour intervals. Peduncle lengths of the experimental animals were greater than those of the control animals. When returned to still water, the peduncles of the experimental animals shortened during the next five hours. Evidence that a similar process occurs under natural conditions is presented in Table I, where animals of similar size are compared for ratio of rachis diameter to peduncle length on the same day in regions subjected to different surge action (deep and shallow water) and in the same region on days of different water velocities. Rachis diameter and peduncle length were measured as in the laboratory. The results demonstrate a significant increase in peduncular lengths in the same area of bottom on days of increased surge, and among animals in the nearshore, turbulent region compared to those from deeper, quieter, water.

There are limitations to anchoring. The colony can be uprooted when strong water currents lift the edge of the rachis off the bottom and push on its surface. Since a large rachis offers a larger surface on which the water can act, a larger peduncle is necessary to withstand uprooting. While maximum peduncle extension increases with rachis diameter during growth, the ratio between peduncle length and rachis width is not constant over the size range, and small sea pansies have proportionally longer peduncles than larger colonies (Table II). As a result, smaller colonies can remain anchored in swifter water than larger ones. Field evidence to this effect is presented in Figure 5. Various-sized stained sea pansies were released in compact groups in regions of different water velocities. The animals were positioned upright on the bottom but not covered with sediment. The center of the group was marked by a stake driven into the sand. Between 30 and 60

TABLE I

*Mean ratio of peduncle length to rachis diameter at various positions along depth gradient and under various surge conditions. "Calm" was when surf height was 0.4 meters; "rough" was when surf height was 1.4 meters. Samples varied in number from 60 to 150 colonies. Sample means of same size class at different surge and different depth differed significantly. Sample means of different size classes at same depth or same surge condition also differed significantly ($P < .01$; ANOVA and one-sided *t*-tests).*

Surge condition	Depth of sample	Size class of sea pansy (in mm)		
		21-40	41-60	61-80
Calm	6.0 meters	1.36	1.08	0.83
	12.0 meters	—	0.92	0.74
Rough	6.0 meters	2.82	1.75	1.36
	12.0 meters	—	1.26	1.10

TABLE II

Maximum extension of peduncle in relation to diameter. Small animals can extend their peduncle proportionally more than large colonies.

Rachis diameter (mm)	Peduncle length (mm)	P/R ratio
10	28	2.80
20	71	3.55
30	77	2.57
40	83	2.08
50	87	1.74
60	89	1.48
70	96	1.37
80	94	1.17
90	96	1.06
100	94	0.94

minutes after release a polypropylene line marked in meters was swung in a circle around the stake. The distance of each animal from the stake and its shoreward-seaward position with respect to the stake were recorded. The released animals were thus monitored for the following seven days. The results show that larger colonies were lost from the shallow, swift water location while smaller individuals were not. On the other hand, in the deeper, quieter release area, similar proportions of both large and small animals were recovered. Furthermore, laboratory experiments showed that a current strong enough to uproot large colonies did not uproot smaller ones. Two animals of different sizes were placed in an aquarium equidistant from the source of a water current of known velocity. Current velocity was steadily increased until both were uprooted. The current velocities used were similar to those in the study area. In all 40 tests the larger experimental animal was uprooted first.

The autozooids. The autozooids, buffeted by water currents and moving sediment, frequently strike both the rachidial surface and each other. This buffeting does not cause their withdrawal. Individual polyps remained extended at least an hour while the colony was subjected to either the strong, oscillating flow of wave surge or strong unidirectional currents in the laboratory. In the laboratory, although sustained water movement did not cause polyp withdrawal, a sudden increase in flow across the colony causing a sharp flexure of the rachis resulted in polyp retraction. The retraction of polyps in response to water movement was thus mediated by events affecting the rachis. Rachidial flexions by water movement in which the edge of the rachis is gently lifted off the bottom are commonly seen in the field; many of these flexures, however, are not associated with polyp withdrawal.

Colony response: anchoring. Field experiments demonstrated a characteristic behavioral pattern subsequent to uprooting and preparatory to reanchoring. The sequential events following uprooting are: (1) retraction of all expanded polyps; (2) retraction of the peduncle; (3) expulsion of the water from the colony, thus flattening the rachis (Fig. 2b); (4) settling on the substrate; (5) peduncle expansion and insertion into the substrate, and (6) re-expansion of the rachis and

re-extension of the autozooids. Polyp retraction occurs within five seconds of uprooting. Peduncle retraction also begins within a few seconds but is not completed as fast. Ninety-five per cent of the colonies reached complete peduncular retraction within 30 seconds after uprooting. Although expulsion of water always follows polyp retraction, it may not begin for 20 seconds after uprooting. Expulsion, once begun, was accomplished within 10 seconds. After expulsion the rachis was very much flatter (height/diameter = 0.05 to 0.08) than any resting animal (height/diameter = 0.1 to 0.5; Fig. 2a, b). The retraction and expulsion processes occurred as the animal was buffeted along the bottom by wave surge. Only when the rachis was completely flattened and had landed "polyp-side up" on the bottom, usually in the trough between two sand ripples, did the colony escape movement by water currents and become stationary. The time between uprooting and anchoring position varied with surge strength but averaged 3 minutes over a range

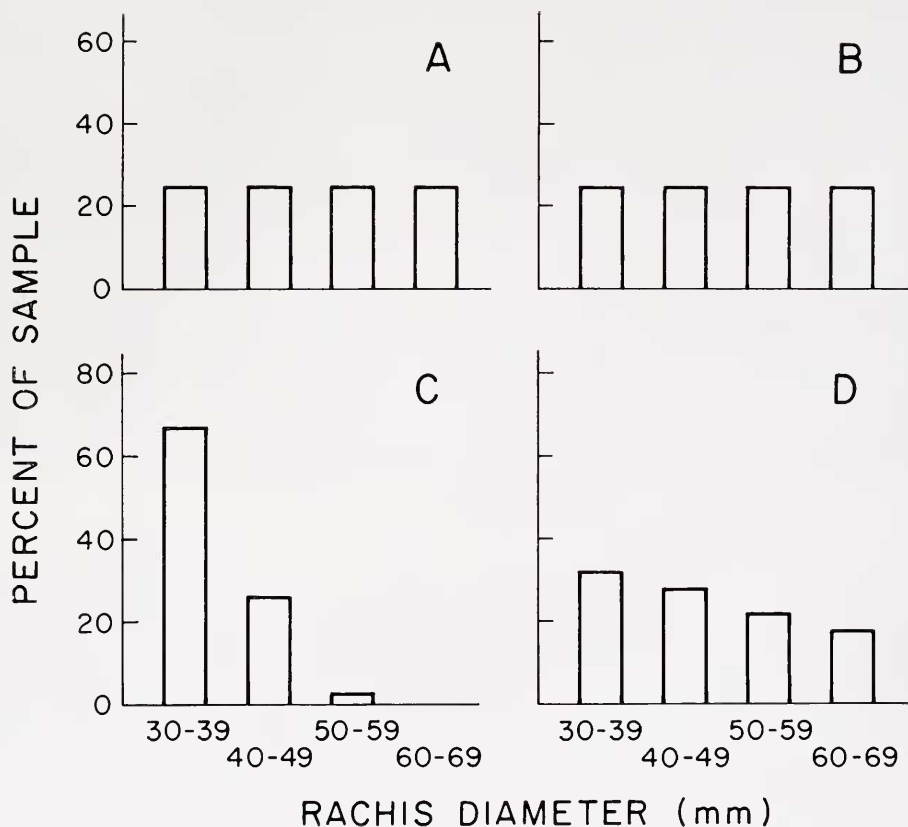


FIGURE 5. Mark-and-release experiment demonstrating differential anchoring ability of various sized colonies. Initial size distributions of groups released in shallow (A; $n=100$) and deep (B; $n=100$) water. All animals were measured within six square meter area around release point. Size distribution of released animals one week later are given in C (shallow; $n=33$) and D (deep; $n=78$). The C and D distributions differ significantly ($P < 0.001$; chi-square test), and demonstrate better anchoring ability of small colonies.

TABLE III

Laboratory emergence rates of buried *R. kollikeri*. The colonies tested ranged in diameter from 35 to 45 mm.

Amount of sand (in cm) placed on experimental <i>B. kollikeri</i>	Mean time to emergence (in minutes)	Successes per 15 trials
1.0	25 ± 7	15
2.0	55 ± 16	15
3.0	92 ± 26	15
4.0	145 ± 38	12
5.0	190 ± 45	8
6.0	215 ± 62	10
7.0	240 ± 79	6

of surge conditions. Reanchoring was a lengthy process. The time to peduncle insertion varied from 15 minutes to several hours. After the peduncle had begun insertion, the rachis expanded and the polyps emerged.

Colony response: emergence. In addition to the anchoring problem, *Renilla* must deal with burial by shifting sediments. The small, constant rain of sediment normally encountered was removed by mucous strands which entangled sand grains and were then swept off the rachis by water flow and small rachidial movements. This rachidial clearing was also seen in the laboratory.

Occasionally, however, large amounts of sand are deposited on *Renilla*. Laboratory studies demonstrated that sea pansies could dig themselves out of 7.0 cm of sand. The rates of emergence varied among individuals but averaged 2.0 cm per hour (Table III). To observe the digging behavior, animals were placed in a glass cylinder of slightly larger diameter. The digging involved rachidial waves which began at the insertion of the peduncle and moved around the edge of the rachis. By flexing the rachis, sediment from above slipped below and became the surface against which the next series of waves pushed.

Interactions with predators

The sea pansy behaviors discussed so far have concerned interactions between the animal and its physical environment. The sea pansy also avoids predators behaviorally. The two principal predators of *Renilla* in southern California are the asteroid *Astropecten armatus* (a generalist feeder) and the nudibranch *Armina californica* (a pennatulid-specific feeder). *Renilla* employs different means to repel attack from these predators.

Astropecten armatus. The sea pansy fends off asteroid attack with its expanded autozooids. When the asteroid touches a polyp of a colony, it quickly lifts its arm away and often changes its direction of movement. In 200 field and laboratory observations sea pansies with expanded polyps were invulnerable to asteroid attack. However, when expanded colonies were manipulated and the polyps caused to retract, *Astropecten* crawled over the colony and began ingestion. *Astropecten* is also limited to preying upon *Renilla* of approximately 40 mm or less in diameter. Only colonies of this size have been found in the gut of the

asteroid(Fig. 6). This limitation is due to *Astropecten* digesting prey within its body cavity rather than outside as many asteroids do.

Once a sea pansy was ingested by *Astropecten*, extrusion of the polyps did not effect the asteroid. The small extruded portion of the asteroid's stomach observed during ingestion showed no apparent reaction throughout 15 minutes of sustained contact with expanded polyps. However, the stomach tissue did withdraw in response to mechanical prodding and chemical (weak acid and base) stimuli.

Armina californica. *Renilla* displays a specific escape behavior in response to attack by this nudibranch. It effects escape by a specific set of sequential behaviors seen in both field and laboratory (Fig. 7): first, rapid retraction of expanded polyps; secondly, concomitant peduncular retraction; thirdly, initiation of a rachidial flexion which proceeds around the margin of the rachis; and fourthly, a characteristic fixed rachidial contraction which can be maintained for many minutes. By this behavior, the sea pansy allows itself to be uprooted from the substrate and tumbled

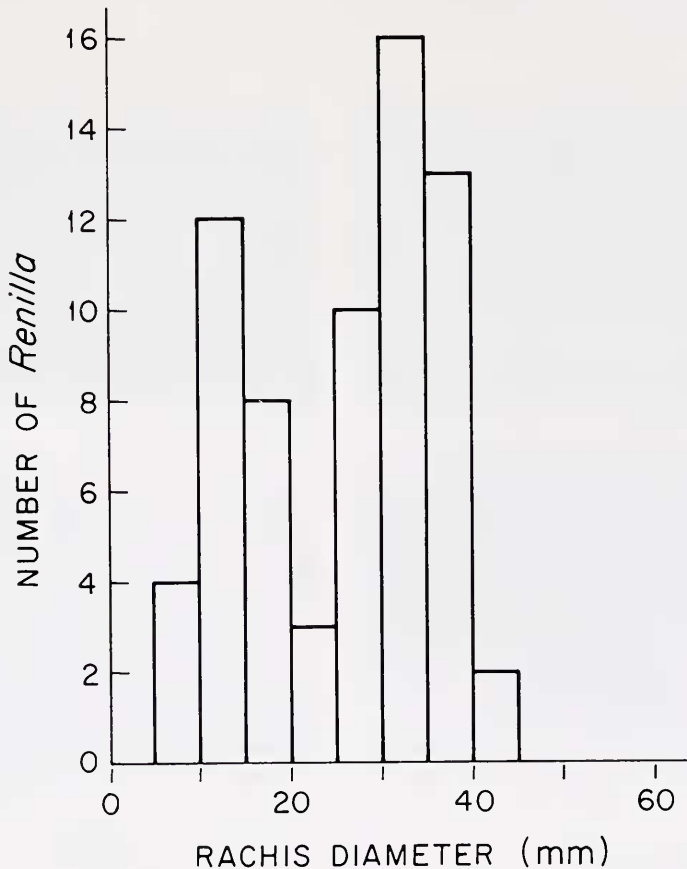


FIGURE 6. Size distribution (rachis diameter) of sea pansies ingested by *Astropecten armatus* ($n = 68$). Note that the two largest colonies were 41 mm in diameter.

away from the predator by water currents flowing along the bottom. The actual removal from the substrate usually occurred as a result of the second and third steps of the above sequence. As the edge of the rachis is lifted off the substrate, a broad area of the rachial surface is exposed to water currents. The rachis is held turgid during these rachial waves in a manner not seen during either the resting state or the flexions associated with sand removal. Given this stiff surface against which to act, the water uproots the animal and tumbles it along the bottom. There was considerable variation from colony to colony in response time but a general pattern was present. Within 5 to 10 seconds after attack the polyps were retracted and the peduncle began retraction. Within 20 to 40 seconds the first rachial wave was initiated. Although the time varied with surge conditions, generally within one or two minutes after first contact with the predator the sea pansy was uprooted. On calm days with little surge, the sea pansy was sometimes not uprooted upon attack.

Figure 8 compares the distances colonies were displaced after attack by the nudibranch and physical uprooting by the experimenter. All trials were conducted on the same day under the same surge conditions. The average movement subsequent to attack was 6.6 meters (s.e. = 0.25), while that following physical

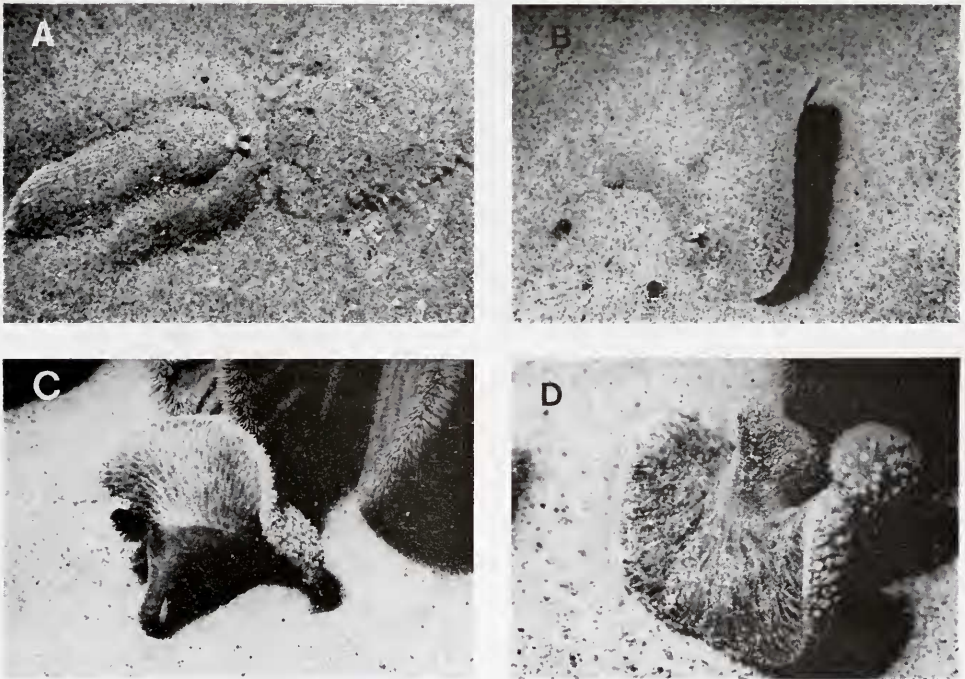


FIGURE 7. Escape behavior from *Armina californica*. A. *A. californica* approaching an expanded sea pansy. Note expanded autozooids. B. *A. californica* contacting *R. kollikeri*. Note retraction of polyps and commencement of rachial wave. C. The sea pansy is being uprooted as rachial waves continue and the peduncle retracts. (Animal in background is the sand dollar *Dendraster excentricus*.) D. Uprooted colony in "saddle" configuration. Note retracted peduncle. The diameter of the *Renilla* depicted is 65 mm.

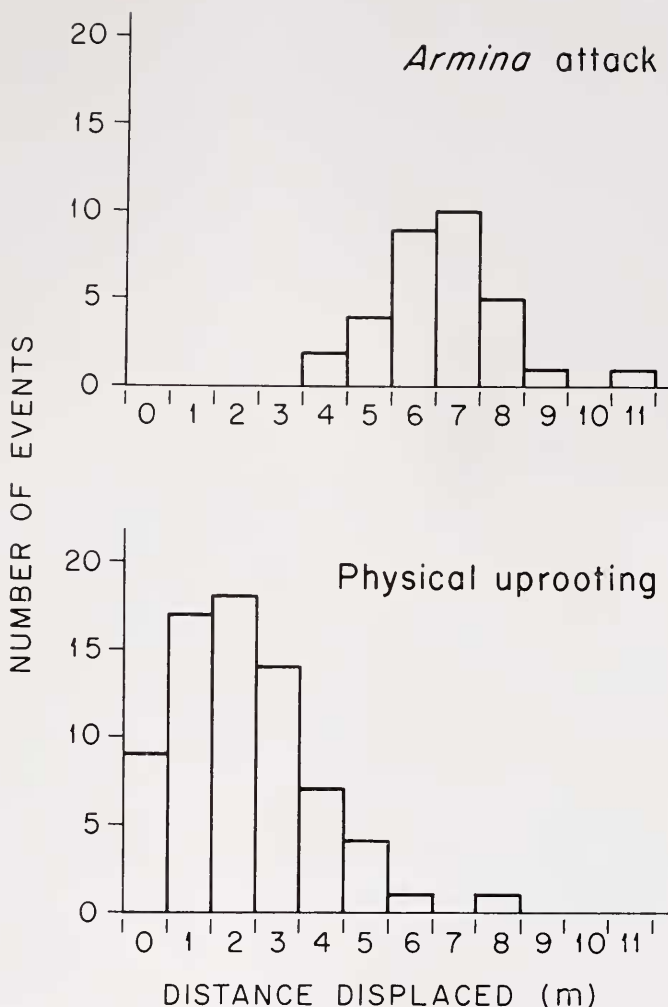


FIGURE 8. Distance between point of (A) attack by *Armina californica* ($n=33$), and (B) uprooting by diver ($n=60$) and point of reanchoring. The distribution means (6.6 m, s.e. = 0.25; and 2.3 m, s.e. = 0.19) differ significantly ($P < 0.001$; Student's t -test).

uprooting was 2.3 meters (s.e. = 0.19). The greater distance displaced while escaping was consistent over a wide range of surge conditions and is due to the persistence of the final rachidial contraction which may be held for several minutes. After relaxation from this configuration, the rachis and peduncle contract and the behavior preparatory to settling and reanchoring begins as described above.

It was not always necessary for the sea pansy to be tumbled away from its attacker to avoid predation. *Armina* is often swept off the colony by surge when the rachis is lifted off the bottom. However, the escape behavior continued after the undibranch was swept away.

The effectiveness of the escape behavior is very high (Fig. 9). Over 95% of observed attacks by *Armina* ended within three minutes. Calm water, however, may thwart the sea pansy's attempt to escape. Figure 9 compares the escape efficiency on a day of moderate water movement (water velocities of about 1.2 meters per second) and on a day of quiet water (velocities of about 0.3 meters per second). Alternatively, if a sea pansy, while tumbling along the bottom, became wedged between two objects on the bottom, (e.g., two sand dollars) it could not repel the nudibranch. Under these conditions colonies were seen with

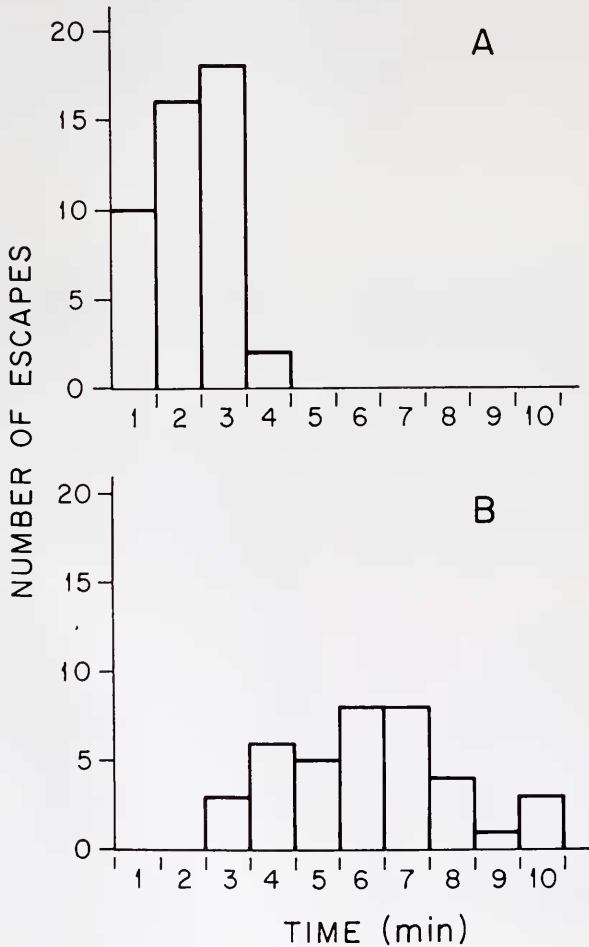


FIGURE 9. Effectiveness of escape behavior from *Armina californica*. The time to prey escape under (A) moderate surge conditions ($n = 44$), and under (B) calm water conditions ($n = 38$) is plotted. Note greater effectiveness of response with greater water movement. Means of distributions (2.3 min, s.e. = 0.12; and 6.1 min, s.e. = 0.31) differ significantly ($P < 0.001$; Student's t -test).

TABLE IV

Specificity of sea pansy escape behavior. All experiments were conducted in the laboratory on anchored and expanded colonies. The "control" was a group of sea pansies in which spontaneous rachidial waves appeared during the period of the experiment.

Animal tested	Number of trials	Number of escapes in 10 min
Echinoderms		
<i>Astropecten armatus</i>	100	1
<i>A. californicus</i>	60	0
<i>Luidia foliolata</i>	80	2
<i>Dendroaster excentricus</i>	100	2
Molluscs		
<i>Armina californica</i>	100	98
<i>Megasurcula carpenteriana</i>	60	5
<i>Nassarius fossatus</i>	60	3
<i>Olivella biplicata</i>	100	2
<i>Polinices altus</i>	75	1
<i>Terebra pedroana</i>	60	0
<i>Hermisenda crassicornis</i>	60	6
<i>Flabillinopsis iodinea</i>	60	4
Crustaceans		
<i>Heterocrypta occidentalis</i>	60	1
<i>Randallia ornata</i>	60	2
<i>Cancer gracilis</i>	100	3
"Control"	100	3

as many as six nudibranchs feeding simultaneously for periods of up to 30 minutes and were usually totally consumed.

The effectiveness of escape behavior was low for colonies smaller than 20 mm in diameter. In spite of escape movements, such colonies were small enough to be either engulfed whole or held on the bottom and consumed by the predator.

Only *Armina* elicited escape behavior of the sea pansy (Table IV). The other animals tested were errant gastropods, crustaceans, and echinoderms found within the study site.

Food and feeding

The sea pansy has difficulty capturing motile prey. In 500 encounters between polyps and 0.4 to 0.7 mm long *Artemia* nauplii, only three nauplii were caught and ingested. Similarly, in 100 encounters between polyps and copepods 0.1 mm long, no copepod was caught. However, if *Artemia* nauplii were heat-killed, *Renilla* caught and ingested them. *Renilla* could also ingest 0.1 to 0.4 mm long bits of ground mussel. The sea pansy also ingested a suspension of single-celled algae. When a colony was placed in a suspension of the alga *Dunaliella* sp., the algae were seen entangled in mucous strands on each autozoid (not on a mucous net stretching between polyps) and passed to the mouth. Within 30 minutes algae were seen within the gut, and they were not expelled within six hours after ingestion.

DISCUSSION

The peak abundance of *Renilla kollikeri* is in shallower water than that of any other sea pen along the southern California coast. Although found in embayed areas, sea pansies are more characteristically members of the subtidal fauna of shorelines exposed to ocean swell. The strong, multidirectional water currents of this region, which greatly alter force and direction rapidly, and the resulting movement of unconsolidated substrate, greatly influence the resident fauna. The sea pansy has morphological and behavioral features which are adaptive to life in this habitat and allow it to exploit regions unsuitable to other sea pens.

Sea pansy morphology is unique among pennatulaceans with respect to a number of features. The autozooids are arrayed on a horizontally expanded rachis, in marked contrast with other sea pens (such as *Stylatula elongata* and *Virgularia* sp., which are abundant seaward and deeper than the peak abundance of *Renilla*) where they are positioned on a vertically expanded rachis. While other sea pens can extend their colonies to as much as a meter or more, the sea pansy can extend to only about 60 mm above the bottom; the maximum thickness of an expanded rachis plus the maximum height of an autozooid. The "low profile" of the sea pansy's rachis is adaptive for life in areas of strong currents since it offers minimal resistance to water flow. This low resistance is expressed by the colony's lack of orientation to water currents. Sea pens such as *Virgularia*, are oriented so that the leading, or ventral, edge of the leaf always faces into the current and turns as the current turns. The sea pansy, whose two large rachidial leaves are held against the bottom, is positioned randomly with respect to current.

In addition to these morphological features, many of the behavioral patterns of the rachis are adaptive to nearshore life. Lowering its curvature in response to increasing water flow minimizes lift forces which act to uproot the animal. Under most field conditions deflation overrides the tendency to inflate and thereby maximizes food-capturing potential. As the center of the rachis is elevated and the upper surface becomes more convex, the zooids on the central portion of the rachis are lifted higher into the water and the volume swept by the feeding zooids increases. The hemispherical feeding surface of the inflated rachis is approximately 25 per cent greater than the deflated rachis of similar diameter.

The response of *Stylatula* and *Virgularia*, which have a vertically expanded rachis, to increased surge action is to withdraw into the substrate to varying degrees. Because the feeding polyps of these sea pens are vertically arrayed, the extent of the feeding surface, and hence, the feeding ability of the colony is greatly altered by any change in the rachis extension. *Renilla*, with its horizontal array of autozooids, does not decrease the number of feeding polyps under increasing water flow.

Peduncular morphology is also adaptive for life in turbulent waters. The peduncle of the sea pansy is very extensible (see Table II) and flexible. This flexibility is afforded in part by the absence of the incompressible skeletal rod present in the peduncle of most sea pens (the genus *Renilla* is not unique in lacking a rod, and other genera, e.g., *Ptilosarcus*, have reduced rods, but these conditions are highly aberrant among pennatulaceans; see Kukenthal, 1915). While this greatly expanded peduncle imparts a high degree of anchoring ability, a better index of anchoring ability is the ratio of rachis height (length) to peduncle length.

Sea pens with an elongated rachis would presumably need a larger peduncle to compensate for increased water resistance. Sea pens with a large peduncle relative to the height of the rachis, would have the greatest anchoring ability. *Renilla* has the lowest rachis height/peduncle length ratio (0.08) of any genus of sea pen found in the world (measurements of the ratios of sea pens not found locally were derived from the monographs of Kukenthal, 1915; Kukenthal and Broch, 1911; Hickson, 1916).

The anchoring abilities of the sea pansy not only allow it to utilize a region of substrate not exploited by other sea pens but also determine several aspects of its own distribution. The inshore boundary differs for each size group of sea pansy within the population because larger animals cannot remain anchored as well as smaller animals (Fig. 5). The differential ability of small individuals to inhabit the inshore limits of the sea pansy distribution plays an important role in the maintenance of the population as young animals inhabit areas too turbulent for effective foraging by predators. The young prey in this nearshore refuge are a source of recruitment to the offshore population of *Renilla* (Kastendiek, 1975).

In addition to maintaining its position on the bottom, the sea pansy must deal with being buried by shifting sediment. The amount of suspended sand varies with the depth of water and the strength of the wave surge. During storms the level of sediment in the shoreward limit of the sea pansy distribution can be altered by as much as 30 cm in 24 hours. *Renilla* can dig itself out of large deposits of sand suddenly placed upon it. It does so with repeated waves of rachidial flexure which sweep around the margin of the colony. Smaller deposits of sediment are cleared from the rachidial surface by the combined effects of rachidial flexures and mucous streaming. Emergence from deposits of sand and maintenance of clean surface by such mucous streaming has been reported previously among a number of corals (Yonge, 1930). One study (Marshall and Orr, 1931) suggests that the ability of a fungid coral, *Fungia* sp., to clear its upper surface of large deposits of sand enables the animal to move up through a column of sediment.

When *Renilla* is uprooted from the substrate in the field, it is generally advantageous to become re-established as quickly as possible. Prolonged buffeting may damage the colony or transport it to less favorable environments (*e.g.*, the surf zone). The most striking feature of the re-establishment behavior is the complete rachidial deflation. The degree of water expulsion from the colony is much greater under these conditions than under any other. Sand often accumulates on the surface of reanchoring animals. This layer may aid reanchoring but in the laboratory it was not necessary. The anchoring is completed with the inflation and insertion of the peduncle, which can occur while the rachis remains deflated. This ability allows anchoring to proceed while the colony is still unaffected by water movement. The process by which the peduncle digs into the substrate is similar to the process by which the sea anemones *Peachia hastata* (Ansell and Trueman, 1968) and *Phyllactis* sp. (Mangum, 1970) burrow. Peristaltic movements of a swollen region of the peduncular column travel from the distal end of the peduncle toward the rachis. Similar peristaltic movements in the rachis and peduncles of other sea pens have been described (Musgrave, 1909; Titschack, 1968).

Like the sea pansy, rod-bearing sea pens must also be stationary on the bottom to reanchor, but the morphology of these animals makes them much more sus-

ceptible to movement by water. In areas of high water velocities (greater than 2 meters per second) *Renilla* can reanchor much faster than *Stylatula*. Again, the sea pansy's low profile appears adaptive in regions of strong wave surge.

Sea pansy morphology is also influential in escape from the predatory nudibranch, *Armina californica*. Some pennatulaceans, (e.g., *Ptilosarcus guerneyi*, *Stylatula* and *Virgularia*) contract into the substrate when attacked. *Renilla* cannot since its flattened rachis prevents rapid withdrawal. The sea pansy avoids predation with a lateral displacement resulting from the use of the water movement it normally avoids. Upon attack the edge of the rachis is lifted and held rigid in the water current above the bottom. The sea pansy uses the rachis as a "sail" in the currents to uproot and tumble away from the attacker, a behavior quite contrary to the behavioral patterns responsible for maintenance of position on the bottom. Both the rigidity of the rachis and the "saddle" configuration (Fig. 7d) are unique to this escape response.

The escape behavior of *Renilla* is specific to *Armina* in the area studied (Table IV). Other anthozoan escape responses (for review see Ross, 1974) have been seen in rock-dwelling sea anemones and have all involved active propulsive movements. Movement in the genera *Bolocerooides* and *Gonactinia* is due to synchronized tentacular sweeps and in *Stomphia* and *Actinostola* to flexions of the column. Even in still water they are capable of moving away from their original position. *Renilla*, however, depends on an external force, wave surge, for its propulsion. Its musculature affects locomotion only by positioning the animal so that the water can propel it. Because of this inability to move, the nudibranch predation on the sea pansy increases when and where surge action is weak (Kastendiek, 1975).

An interesting similarity between the *Renilla* and *Stomphia*, *Actinostola*, *Gonactinia*, (Ross, 1974), *Anthopleura* (Rosin, 1969), and *Ptilosarcus* (Birke-land, 1974) is the sensitivity of the escape behavior to nudibranch predators. As some nudibranch families have evolved specificity in feeding on coelenterates, particularly the families Eolididae and Arminidae, the cnidarian prey which represent widely divergent taxa have convergently evolved escape behaviors.

The other major predator in the study area is the asteroid *Astropecten armatus*. This generalist predator will ingest *Renilla* smaller than about 40 mm in diameter. However the sea pansy is available as prey only when the autozooids are withdrawn. Presumably the nematocyst found in the autozooids are responsible for defending the colony from this predator.

Thus *Renilla* demonstrates two strategies of defense against two different predators: a behavioral escape from *Armina* and an anatomical defense against *Astropecten*. The sea pansy may use its bioluminescence as a third defense mechanism directed against a third predator type—nocturnally foraging fishes. Fish predation on the sea pansy is evidenced by teeth marks found on colonies. As nocturnal fishes have been shown to avoid a bright flash of light (Woodhead, 1966), the light emission of *Renilla* may startle fish who have nipped at the rachis. This quick deterring of the fish would account for the large number of colonies which have only a single bite taken out of them. The invertebrate predators of *Renilla*, however, are not deterred by the bioluminescence.

The feeding activity of the sea pansy is notable for both its means of prey capture and its prey selection. Like most Alcyonaria, *Renilla* is a suspension feeder. However, while an inefficient gatherer of motile animals larger than or as motile as a calanoid copepod 0.1 mm long, nonmotile prey up to the size of *Artemia nauplii* can be captured and ingested.

The sea pansy is also capable of collecting and ingesting unicellular algae. Roushdy and Hansen (1961) observed the ingestion of diatoms by another alcyonarian, *Alcyonium digitatum*, one of the few reports of phytophagy among the largely carnivorous Cnidaria. The suggestion that the sea pansy feeds on algae raises questions concerning food specialization among cnidarians. Previously, food specialization within this group was couched in terms of animal capture (*e.g.*, Yonge, 1930). However, food specialization may also be based on food type (*i.e.*, plant or animal). Increased food sources may lead to a more important role of food specialization in allowing the coexistence of many sympatric species of closely related cnidarians. The two reports of algal ingestion by cnidarians concern alcyonarians. Perhaps this group is largely restricted to feeding upon nonmotile plankton, particularly algae.

Muco-ciliary tracts on the tentacles of the polyps are important in ingesting food. Although tentacle flexures do move bits of food material into the mouth, they are not necessary. During the phytoplankton-feeding experiments a column of the single-celled algae was seen moving down the tentacle and into the mouth. The role of muco-ciliary tracts in the feeding of cnidarians is known from numerous cases (*e.g.*, Yonge, 1930). MacGinitie and MacGinitie (1968) described the use of a mucous net as a feeding structure of the *Renilla* colony. During the present study such a network of mucous strands stretching from one polyp to another was observed in still water but was not used in food capture. Furthermore, a mucous net has not been observed when the colony has been in moving water. It is highly unlikely that a mucous net could persist in the nearshore areas of exposed beaches.

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SUMMARY

1. *Renilla kollikeri* is morphologically adapted to live in turbulent benthic areas by having a horizontally expanded rachis which offers less resistance to water flow than the vertically expanded rachis of most pennatulaceans. Furthermore, the colony is anchored by an extensible and flexible peduncle which is the largest (in relation to rachis height) among the Pennatulacea.

2. *R. kollikeri* has a number of behavioral adaptations to life in turbulent water. In response to increasing flow it alters its rachis curvature and peduncle extension to decrease resistance and increase anchoring, respectively. The sea pansy can emerge from large deposits of sediment suddenly placed upon it. Such shifts in sediment are a common occurrence in its habitat. *Renilla* has a specific

set of behavioral characteristics which re-establish the colony quickly if it is uprooted from the substrate.

3. The anchoring ability of individual colonies, which decreases as the size of the colony increases, allows small colonies to inhabit the nearshore limit of the species' distribution.

4. The sea pansy's unusual morphology contributes to its unusual behavior following attack by the nudibranch, *Armina californica*. The sea pansy positions itself so that it is uprooted from the substrate rather than withdrawing into it. By means of this species-specific behavior, the prey utilizes the prevailing water currents of its environment to avoid predation.

5. The sea pansy defends itself against different predators in different ways. It employs a behavioral escape from the specialist *Armina californica*, and an anatomical feature (presumably the nematocysts of the autozooids) and a size escape from the generalist asteroid, *Astropecten armatus*.

6. *Renilla* is restricted to preying upon largely nonmotile detrital or planktonic material. The utilization of unicellular phytoplankton is suggested.

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